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THE FEEDING-HABITS OF THE ADULT LEPIDOPTERA HETERONEURA

By Maud J. Norris, Ph.D. (Mrs. O. W. Richards).

(Dept. of Entomology, Imperial College of Science and Technology.)

[Read 20th November, 1935.]

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1. Introduction.

During the year 1933 a series of experiments was carried out on the nutritional requirements of the adults of the Phycitid moths *Ephestia kühniella* Z., and *E. cautella* Wlk. These experiments gave some rather curious results, the details of which have been published in another place (Norris, 1934 A). Briefly speaking, it was found that both the longevity and the fecundity (the number of eggs laid) of adult *E. cautella* Wlk. are roughly halved if the moths are deprived of drinking-water, but that *E. kühniella* Z. is only very slightly affected in these respects by lack of water. It was further found that although the longevity of both species was considerably increased if the moths were fed on cane-sugar solution, their fecundity was no greater than if they had been fed on distilled water only. While, therefore, the insects will feed readily on sugars, they derive from them no benefit which can normally be of any survival value. Now adult butterflies feed extensively on the nectar of flowers and it has naturally always been assumed that they cannot live normally without a sugar diet. In view of these experiments with *Ephestia*, however, it seemed necessary to prove that the butterflies really do require the sugars and not merely the water of which nectar is so largely composed. During the summer of 1934 a small-scale experiment was carried out on *Pieris rapae* L., the Small

Cabbage White butterfly. The results of this experiment verified satisfactorily the truth of the usual assumption—at least for this species. The details of the experiment have been published (Norris, 1935 B).

On the considerations briefly summarised above the Lepidoptera Heteroneura may be roughly divided into the following groups :—*

A. Those which require both sugar and water for normal longevity and reproduction, *e.g.* at least some Rhopalocera.
B. Those which require water but not sugar for normal longevity and reproduction, *e.g. Ephestia cautella* Wlk.
C. Those which can imbibe liquids but which require neither water nor sugar for normal longevity and reproduction (hypothetical).
D. Those which have the mouth-parts atrophied and are incapable of taking any nourishment *e.g. Bombyx mori* L., *Lymantria dispar* L., etc.

While the existence of these groups is established the number of Lepidoptera which can be assigned to their correct group is, in the existing state of our knowledge, exceedingly small. Experimental work on the actual *food-requirements* of the adult Lepidoptera is very small and is almost entirely confined to work on a few economically important species; such work has already been summarised (Norris, 1934 A). Concerning the *feeding-habits* of the adult Lepidoptera, on the other hand, a considerable number of observations have been made. Tutt (1897) refers to a number of these in his paper on the drinking-habits of butterflies and moths, but for the most part the records are scattered throughout the literature in a highly inaccessible form. In the absence of sufficient data on food-requirements it seemed desirable to collect together in one place as much as possible of what is known about feeding-habits. Such a survey suggesting, as it does, various probabilities as to food-requirements, should provide a useful basis for future work in this field. The summary is necessarily very incomplete, the observations of Lepidopterists being frequently published as short notes, often without titles, in the proceedings of innumerable societies. It has consequently only been possible to collect together a mere fraction of the observations which must have been published, in the hope that the sample will be sufficiently representative to illustrate all essential points. It must also be remembered that there exists a large body of traditional entomological knowledge which does not necessarily find its way into the literature. It is, therefore, quite possible that the experienced Lepidopterist may be able to supply answers to some of the questions which I have had to leave unanswered.

The classification of the Lepidoptera used in the review is, for all practical purposes, that recommended by Imms (1934). An attempt was at first made to standardise the nomenclature used by referring to various standard systematic works, but it was found that the result of substituting the correct names for those used by the original authors would merely be to confuse the general reader and to render the references to published work needlessly obscure. It may therefore be taken that the name mentioned is that employed by the author to whose work reference is made; in a few instances it has, however, been necessary to add the correct name in brackets in order to avoid confusion arising from referring to the same insect under more than one name in different parts of the review.

* This question is discussed in greater detail in a previous paper (Norris 1934 A), and is only summarised here so far as is necessary to explain the *raison d'être* of the present publication.

It became evident from the outset that, with the exception of a few economically important insects, practically nothing was to be discovered concerning the feeding-habits of the Microlepidoptera. Lepidopterists seldom record these insects as being captured while feeding at flowers or at "sugar," but this negative evidence is of little value as in most cases they would probably be ignored. Where they are needed for collections they are more usually obtained by breeding.

2. Nectar.

It is a matter of common observation that the majority of adult butterflies spend a great deal of their time feeding on the nectar of flowers, and it is not intended to pursue this subject here in any detail. Exceptions to this condition will be mentioned later. In view of the difference in habit which often exists between the sexes in the Lepidoptera, it would be interesting to know whether males and females feed on nectar with equal activity. At present there are practically no data which throw any light on this question, the sexes of butterflies caught being seldom recorded. Exceptions to this rule are found in the work of Robertson (1929) and Fritsch (1928, 1930, 1931 and 1932) where the sexes of Rhopalocera visiting flowers are in some instances recorded. These records do little more than show that, as might indeed be supposed, both sexes do frequent flowers to some extent; they are insufficient to give any idea as to the relative frequency with which they do so.

The position as regards nectar feeding in the Heterocera is very much less clear. It is highly probable that a great number, possibly the majority of species, do not feed at flowers but either take no food at all, or take water only. The subject is to some extent discussed by Ord (1899). He includes among the flower-frequenting Heterocera the Sphingidae, the Noctuidae and the Pterophoridae, among the non-flower-frequenting Heterocera the Bombycidae (except *Thyatira batis* L.), the Geometridae (except *Larentia Eupithecia, Anticlea, Iodis, Cidaria,* etc.) and the Pyralidae (except *Pionea* and *Scopula*).

A list has been made of the Noctuids and Geometrids (British species only) mentioned as visiting flowers in the following publications:—Ord (1899), South (1907–1908), Langlois (1925), Robertson (1929) and Tutt (1901–1905). A very rough analysis of these lists, which need not be given here in full, gave the following results:—

Noctuidae:	113	species	belonging	to	62 genera.
Geometridae:	29	„	„	„	15 „

According to Meyrick (1928) the British Noctuidae number about 345 species and the Geometridae about 283 species.* Thus about a third of the total number of British Noctuids are included in these records and only about a tenth of the total number of Geometridae. Needless to say these numbers represent only a fraction of the nectar-feeding species belonging to the two families. Many of the rarer species are probably not included, and in many of the records the genus only is given, in which case the reference was considered as being to one species only. This objection holds good, however, for both families equally, and it seems reasonable to suppose that, as stated by Ord, the nectar-feeding habit is more general among the Noctuids than among the

* In this calculation the Noctuidae include Meyrick's Caradrinidae and Plusiadae and the Geometridae include his Sterrhidae, Geometridae, Hydriomenidae, Monocteniadae and Selidosemidae.

Geometrids. Species of *Tephrosia* and *Hybernia* may be added to Ord's list of the flower-feeding Geometrids.

The Sphingidae are notable nectar-feeders, but exceptions are *Smerinthus* and *Dilina* where the proboscis is reduced, and in *Acherontia atropos* L., which has the proboscis adapted to stealing honey from bee-hives. Among the Arctiidae, at least some of the " Footmen " moths or Lithosiinae seem to be nectar-feeders; Tutt (1901–1905) records *Lithosia complana* L., and *Oenestis quadra* L. as being flower-visitors. According to South (1907–1908) the " Tiger moths " or Arctiinae have an imperfect proboscis and do not visit flowers. As regards the feeding-habits of the Notodontidae no information has been found, but South observes that they are seldom obtained except at light traps, and Tutt (1901–1905) has no record of their being taken either at flowers or at " sugar." The tongue is known to be rudimentary at least in *Stauropus fagi* L. and in *Dicranura vinula* L.; it is probable that most members of this family do not feed. The Lymantriidae have the proboscis reduced and so also have the majority of the Bombycoidea including the Lasiocampidae, the Saturniidae and the Bombycidae. The proboscis is likewise reduced in most of the Psychoidea but not in the Zygaenidae, and South describes *Ino globulariae* Hb. and *I. statices* L. as being flower-feeders; species of *Zygaena* are well known as flower-feeders.

As has been pointed out before, evidence as to the feeding-habits of the Microlepidoptera is practically non-existent. In the course of this investigation flower-feeding records have been obtained only for eight species of Pyraloids, three Tineoids, one Tortricid and one Pterophorid. It is probable that the majority of the Microlepidoptera do not feed on nectar, but it is, on the other hand, very unlikely that the habit is as rare as might be supposed from the exceedingly small number of records quoted above.

No data concerning the sexes of Heterocera taken at flowers has been forthcoming.

The British wild flowers which are most characteristically visited by the crepuscular and nocturnal moths are the following :—ivy (*Hedera helix*), sallow (*Salix* spp.), campions (*Silene* and *Lychnis* spp.), wild sage (*Salvia* spp.), wild thyme (*Thymus serpyllum*), ragwort (*Senecio jacobaea*), knapweed (*Centaurea nigra*), thistles (*Carduus* spp.), hemp agrimony (*Eupatorium cannabinum*), rush (*Juncus* spp.) and sedge (*Carex* spp.). Ord (1899) observed that sallow, ivy and ragwort attract more moths than all the others put together, and these are certainly the flowers most worked by collectors. It is doubtful whether sallow and ivy are really specially attractive or whether their popularity is merely due to their flowering in the spring and autumn when few other flowers are available. Favourite garden flowers are berberis (*Berberis vulgaris*), tobacco (*Nicotiana* sp.), pansy (*Viola* spp.), golden rod (*Solidago* sp.), and valerian (*Valeriana* spp.).

It is a matter of controversy how far the Lepidoptera are attracted to flowers by scent and how far by sight. It is noticeable that most of the flowers which attract nocturnal moths are highly scented and not necessarily conspicuous; Knoll (1927), however, showed that the nocturnal Sphingid *Protoparce convolvuli* L. was attracted almost entirely by sight to the dark purple blossoms of *Nicotiana*, when it was so dark that they were invisible to the human eye. It is therefore quite possible that nocturnal moths use sight in finding flowers to a greater extent than might be supposed merely on grounds of what the human eye can discern. At the same time it must be remembered that the Sphingidae may be exceptional in this respect. There are various sugary

substances other than flower nectar to which Lepidoptera are attracted definitely by scent alone. Included in this category are rotting fruit, the outflowing sap of trees and other plants, aphid honeydew and the fermented sugar-baits used by entomologists for the capture of crepuscular and nocturnal Heterocera. These substances are attractive on account of the strong smell given off during the processes of fermentation, and experiments with artificial baits show that the liquids, to be attractive, must be in a state of fermentation. The Heterocera are, as a group, much more generally attracted to such substances than are the Rhopalocera and it is probable that the great majority of the sugar-feeding nocturnal moths are, in some degree, so attracted. The work of Knoll (1926) and of Ilse (1928) has shown that the Rhopalocera may be roughly divided into several groups according to the method by which they find their food. Many of the flower-visiting butterflies are attracted to flowers entirely visually; a flower, either up or down wind is sighted and then approached in a direct line, the olfactory sense playing no part in the attraction except, in some cases, when the insect is very near the flower. To this group belong the Pierines and the Papilios. At the opposite extreme are those butterflies which are guided to their food entirely by scent; the food is generally strongly smelling and the insects approach it with a probing, zigzag flight. Examples of this are found in the Nymphalines *Charaxes jasius* L. and *Apatura iris* L., neither of which are known to visit flowers. Under certain conditions some species of *Vanessa* may be similarly attracted by scent alone. According to Ilse (1928) most butterflies belong to an intermediate group where both colour and scent are the attractive agents, the scent calling attention to the flower in the first instance and before it is actually seen. It having been shown that certain members of the NYMPHALIDAE are more responsive to odours than other Rhopalocera it is not surprising, as will be seen in succeeding sections of this paper, that most of the butterflies which visit strongly smelling but visually unattractive substances belong to this family. This question will be more fully discussed in a later section.

3. OVER-RIPE AND ROTTING FRUIT.

A number of Lepidoptera are strongly attracted to the sweet juices of over-ripe fruit, either while it is still on the plant or after it has fallen to the ground. In temperate countries the chief frequenters of rotten fruit are the NOCTUIDAE, and Tutt (1901–1905) says that ripe yew-berries in the autumn attract nearly all the species which normally visit the flowers of the ivy. Ripe blackberries and plums are also particularly attractive to Noctuids. Hewett (1888) describes how, on one occasion, the absence of moths at artificial sugar-baits was explained when they were found swarming over the ripe fruit in a neighbouring plum orchard; 15 species of Noctuids were taken on the fruit. Barrett (1900) mentions 40 species of Noctuids taken feeding on damaged peaches in South Africa. The most characteristic British fruit-feeders, to judge from the frequency with which they are recorded by different workers appear to be *Anchocelis pistacina* Fb. (on yew-berries), *Dasycampa rubiginea* Fb. (on yew-berries), and *Gonoptera libatrix* L. (on blackberries). South (1907–1908) describes the Nolid *Sarrothripa revayana* Tr. as feeding on ripe blackberries, but apart from this no references have been found to Heterocera, other than Noctuids, feeding on ripe fruit. The only British butterfly described as visiting ripe fruit to any extent is *Pyrameis atalanta* L. which feeds on plums (Morgan, 1925, South, 1906). Kirby (1894–1897, **1**: 93) stated that *Vanessa antiopa* L.

feeds on fallen fruit. Probably the most consistent butterfly fruit-feeders belong, however, to the non-British genus *Charaxes*. Knoll (1926) has studied the behaviour of *Charaxes jasius* L. in Dalmatia in great detail. Both males and females of this species were observed to feed mainly on ripe figs, grapes, and the fruits of *Solanum lycopersicum*. They never visited the neighbouring *Erica* flowers on which swarms of other Lepidoptera were feeding. Other observers agree that these butterflies never visit flowers. De Nicéville (1895, *J. asiat. Soc. Bengal*, **64**), describes all species of *Thaumantis* and *Mycalesis*, *Zeuxidia aurelius* Cram. and *Euthalia dirtea* Fab. as frequenting fruit juices. *Morpho hecuba* L. has been seen feeding on rotten bananas (Moss, 1933), and Seitz (1894) saw *Neptis aceris* Cram. on a fruit-barrow in Tokyo. There is no mention on this habit in connection with any species of butterfly outside the Nymphalidae.

4. Juices of Sound Fruit (fruit-piercing).

Some Lepidoptera have the habit of piercing the rind of fruit with the proboscis and sucking out the juices. These fruit-suckers are most frequently reported from Africa, where citrus fruits, apples and peaches are attacked. Unripe fruit is often attacked and the decay resulting from the punctures made by the insects may cause serious damage to crops. The true fruit-suckers nearly all belong to the Noctuidae, important African species being *Ophideres materna* L., *O. fullonica* L., *Aletia argillacea* Hb., *Achea lienardi* Boisd., and *A. catocaloides* Gn. Hargreaves (1929) records the habit for six Gold Coast species of Noctuidae, and Brain (1929) records it for six South African species. The species mentioned by these authors and not included in the above list are the following:—*Hypocala rostrata* Fab., *Erebus walkeri* Butl., *Dermaleipa rubicata* Holl., *Sphingomorpha chlorea* Cram., *Serrodes partita* Fabre., and *Anna tirhaea* Cram. *Ophideres materna* L. and *O. fullonica* L. are the principal fruit-suckers in India (Susainathan, 1924) and also in Australia (Tillyard, 1926). As Leefmans (1932) has pointed out, many records of fruit-sucking may really refer to moths which do not themselves puncture the fruit but merely suck at the holes previously made by the true fruit-suckers such as *Ophideres*. For this reason records of fruit-sucking on the part of any species must be regarded with suspicion unless detailed observation of the feeding processes or morphological examination of the proboscis has been made. Leefmans (1932) has described the proboscis and method of feeding in *Ophideres fullonica* L. The moth settles on the fruit with outspread wings and the head is moved up and down quickly, the stiff serrated tip of the proboscis acting meanwhile as a drill. Breitenbach (1877) pointed out that the teeth on the proboscis of *Ophideres* point backwards and only tear the fruit tissues during the outward movement. Further, one half of the proboscis is a little shorter than the other so that the sharp tip is rendered as fine as possible. It is unlikely that any species of Lepidoptera having a perfectly typical proboscis could pierce the skin of any fruit, much less the tough rinds of unripe citrus fruits. The tip of the proboscis must at least be stiffer and more pointed than is the general rule, even although serrations, as in *Ophideres*, may not be present. Brain (1929) only states that the tip of the proboscis is modified in *Ophideres* and *Serrodes*, but it is not clear whether or not the proboscis of the other species mentioned was examined.

The fruit-sucking habit is infrequent among the Rhopalocera, but Howard (1909) describes how a whole crop of apples and some quinces in east Africa

were ruined by the attack of the adults of the Nymphalid *Crenis boisduvali* Wallgr. The butterflies sucked all the juices out of the fruit and the action of puncturing the rind was actually observed. Decay set in and the fruit fell to the ground, after which the butterflies continued to feed on the decaying mass. The same author describes a similar attack by *Charaxes neanthes* Hew. and *C. zoolina* Westw. on oranges. Hundreds of the butterflies were present, and as many as seven or eight were often seen on one fruit. Howard stated that he was unable to find any other references to Rhopalocera damaging fruit in this manner. Knoll (1926) observed *Charaxes jasius* L. piercing holes in the ripe fruits of *Solanum lycopersicum*; it is therefore probable that the habit is more or less characteristic of the genus *Charaxes*.

5. Exuding Sap of Plants.

The exuding sap of wounded trees is very attractive to a number of Nymphalid butterflies. There are many records of the butterflies feeding to excess on these liquids and becoming completely intoxicated and incapable of flight. The literature of this subject has been reviewed by Fox Wilson (1926). The British species most commonly found at the sap of oaks and willows is *Pyrameis atalanta* L., which is also the butterfly most often found on rotten fruit. There are also a few British records for *Vanessa antiopa* L. and *V. polychloros* L. (Benson, 1877; Peachall, 1900); other species mentioned by Fox Wilson as feeding on sap in Europe are *Vanessa c-album* L., *Limenitis camilla* Schiff., *Argynnis pandora* Schiff., *Apatura iris* L. and *Satyrus* spp. One Lycaenid, *Zephyrus quercus* L., is mentioned. Knoll (1926) and Trimen (1862–1866 : 166) describe the fruit-feeding *Charaxes* as being much attracted to sap, and Carpenter (see Poulton, 1918) saw six east African *Charaxes*, all of different species, feeding at one time on the sap of a tree. Various references to other tropical sap-feeders are made by De Nicéville (1895) and Kirby (1894–1897); the species referred to belong, without exception, to the Nymphalidae. It is remarkable that the Noctuidae, which are the predominant visitors at most sugary fluids, are hardly ever recorded from sap. Fox Wilson (1926) found several unspecified Tortricids caught in sap, but states that few Heterocera were actually found feeding on it; species of *Catocala*, *Plusia* and *Triphaena* are the only ones mentioned in his review. It is, however, highly likely that this peculiarity may be due to the trees having been observed mainly during the daytime.

6. Honeydew.

The sweet secretion of Homoptera, known as honeydew, has frequently been found to attract enormous numbers of Noctuids. Pittoni (1923) gives a list of 37 species of Noctuids taken at the honeydew of aphids on a peach tree in Austria. Nearly all the species were also taken at artificial sugar-baits in the same neighbourhood. Further lists of Noctuids taken at honeydew are given by van Duzee (1885) and by Manson (1931). None of these workers mention any species outside the Noctuidae. Thorpe (1928) in carrying out some experiments with adults of the Tineid *Hyponomeuta cognatella* Tr. observed that the captive moths frequented certain shoots of the food-plant which happened to be infested with aphids. They moved about actively with the proboscis extended, prodding at the leaves; when an aphid was touched with the proboscis a drop of honeydew was exuded and was immediately sucked up by the moth. It was observed that the moths did not seem to stroke the

aphids intentionally but merely to prod them more or less by accident. Martelli (1916) describes the Pyralids *Glyphodes unionalis* Hb. and *Zelleria oleastrella* Mill. as feeding on the excretions of olive scale insects. Jack (1885) records having found the Nymphalids *Vanessa antiopa* L., *Limenitis arthemis* Drury and *L. disippus* Godt. drinking honeydew. The most remarkable honeydew visitors are, however, to be found among certain LYCAENIDAE. This relation between Lycaenids and aphids has been fully discussed by Clark (1926); it is believed to be in some way connected with the larval habit developed in some members of this family of living carnivorously in ants' nests. The species mentioned by Clark belong to the genera *Gerydus*, *Allotinus* and *Megalopalpus*. Poulton (1912) recorded the habit for *Epilota honorius* Fal. and *Hewitsonia boisduvali* Hew. These butterflies settle among the aphids, usually in company with ants, and suck up the honeydew. An early record of the habit is found in Bingham, 1907, *Fauna of British India*, **2**: 287–288, where the observations of H. J. W. Barrow on *Allotinus horsfieldi* Moore are described. The butterfly was seen to stroke the aphids with the proboscis just as the ants do with their antennae. Similar stroking motions were observed by Roepke (1918) in *Gerydus boisduvali* Moore. Clark (1926) found that, at least in *Megalopalpus zymna* Doubl. & Hew., the habit was equally common among males and females.

7. HONEY.

The Death's Head Hawk-Moth, *Acherontia atropos* L., instead of visiting flowers for nectar, as is the habit of other Sphingids, enters the hives of bees, pierces the wax opercula of the cells and sucks out the honey. The habits and morphology of this insect have been described by d'Herculais (1916). The particularly robust proboscis is much sclerotised and sharply pointed, so that it is well adapted to piercing the honey cells. A curious feature is that the aperture of the proboscis, through which the fluid enters, instead of being terminal is situated dorsally a little behind the tip. Hering (1926 : 126) states that *Amorpha populi* L. and *Sphinx ligustri* L., are also honey-stealers. This, however, seems rather dubious, since Meyrick (1928) describes the proboscides of both these species as being imperfect. No further records of the occurrence of this habit in other species of Lepidoptera have been traced.

8. ARTIFICIAL SUGAR-BAITS.

One of the commonest methods of catching nocturnal and crepuscular Heterocera is by attracting them to fermented sugar-baits. This is employed both as a means of catching them for collections and also as a means of pest control. There is an enormous literature dealing with this subject, and it provides a very valuable source of information concerning feeding-habits. It is true that the moths which come to the sugar-baits are attracted by an artificial medium, but their presence there indicates that they do normally feed on one or more of the natural sugary substances mentioned in the preceding sections. Generally speaking, the records of economic trapping experiments give the best details concerning the numbers of moths caught, the proportions of the sexes, the chemical nature of the baits and so on, while it is necessary to consult collectors' records for variety of species.

The baits, to be attractive, must be in a more or less fermenting state, although they have sometimes been found to be more attractive during the

early than during the later stages of fermentation. The moths are attracted to the baits by their olfactory sense only—needless to say there can be no question of visual attraction—and since unfermented sugars are practically odourless it is natural that they should not be visited to any great extent. The chemical factors involved have been experimentally investigated by many workers. Important examples of such work have been published by Frost (1926, 1928 and 1929) and by Peterson (1925 and 1927), both working with the Tortricid *Cydia molesta* Busck, and by Eyer (1931) working with *Cydia pomonella* L.

It is noticeable that the nocturnal sugar-visitors belong to the same families and often to the same species as the nocturnal flower-visitors which justifies the assumption that the appearance of a moth at sugar-baits indicates that it is normally a sugar-feeder. Thus it is well known that most of the NOCTUIDAE come to the baits, and although there are doubtless exceptional species which do not, it is difficult to discover which they are. Negative evidence in a question of this kind means so little. The only Noctuids definitely stated by South (1907–1908) not to visit sugar are *Heliophobus hispidus* Hb., *Luperina testacea* Hb. and *Acosmetia caliginosa* Hb. Kirby (1882) observes that the genera *Nonagria*, *Cucullia* and *Plusia* are not attracted; this might indeed be expected in the case of *Plusia*, as most of the species are diurnal and the baits are usually employed at night.

The late Mr. R. Adkin was kind enough to give me some unpublished details concerning the species other than Noctuids which were caught during a whole season's sugaring from June to October, 1924. The following is an analysis of this list:—

GEOMETRIDAE:	16 specimens belonging to 10 species.				
TORTRICIDAE:	27	,,	,,	7	,,
PYRALIDAE:	5	,,	,,	2	,,
TINEIDAE:	3	,,	,,	1	,,
PTEROPHORIDAE:	2	,,	,,	2	,,

Considering the enormous number of Noctuids which would be caught during such a season of sugaring this catch is sufficiently meagre to leave no doubt that, just as the majority of nectar-feeders in the Heterocera belong to the NOCTUIDAE, so the majority of the sugar-visitors belong to the same family. The principal sources consulted for records of Heterocera other than Noctuids visiting sugar are the following:—Adkin (1925 and unpublished data), South (1907–1908), Carr (1916) and Tutt (1901–1905). 25 species of Geometrids, 7 Cymatophorids, 6 Arctiids, and 3 Sphingids are mentioned by these workers. Nymphalid butterflies occasionally visit sugar patches during the daytime; Tutt (1897) recorded that the following specimens were taken at sugar at Brockenhurst:—4 *Dryas paphia* L., 1 *Eugonia polychloros* L., 4 *Vanessa io* L., 1 *Pyrameis atalanta* L., 6 *Limenitis sibylla* L., 1 *Apatura iris* L., 4 *Pararge egeria* L., 1 *Epiniphele ianira* L., 1 *E. tithonus* L. and 1 *Enodia hyperanthus* L. Standfuss (1896) said that sugar-baits were visited in the daytime by species of *Apatura*, *Vanessa*, *Pararge* and other Satyrids.

As regards the sexes of the moths caught at sugar-baits, it seems that there is no particular tendency for one sex to preponderate. The exact proportions of males and females caught naturally varies considerably in different instances, but speaking generally males and females are attracted equally. This point is illustrated by the examples given in the following table.

Family.	Species.	% Females caught.	Authority.
Noctuidae.	*Feltia gladiaria* Morr.	50%	Crumb (1929).
,,	*F. ducens* Wlk. and *F. subgothica* Hard.	33·8%	,, ,,
,,	*F. exclamationis* L.	87·1%	Goriainov (1915).
,,	*Noctua badinodis* Grote.	14·4%	Crumb (1929).
,,	*Polia renigera* Steph.	54·5%	,, ,,
,,	*P. oleracea* L.	71%	Lloyd (1920).
,,	*Agrotis ypsilon* Roth.	56·5%, 52·1% and 38·4%	Woodhouse & Dutt (1913).
,,	,, ,,	54·7%	Crumb (1929).
,,	*Lycophotia saucia* Hb.	90%	,, ,,
,,	*Prodenia ornithogalli* Gn.	54·5%	,, ,,
,,	*Euxoa segetum* Schiff.	64%	Dobrovljansky (1913).
,,	,, ,,	19·8%	Goriainov (1915).
Tortricidae.	*Polychrosis botrana* Schiff. and *Clysia ambiguella* Hb.	46%	Lafforgue (1914).
,,	,,	53%	Feytaud (1913).
,,	*Clysia ambiguella* Hb.	65·1%	Moreau & Vinet (1919).
,,	*Cydia pomonella* L.	53%	Fowler (1927).
,,	,, ,,	60%	Spuler (1927).
,,	*C. molesta* Busck.	Approx. 50%	Frost (1926).

Feytaud (1916) working with vine-moths *Clysia ambiguella* Hb., and *Polychrosis botrana* Schiff., observed that the greater the number of traps in a given area the greater was the proportion of females caught. From this he inferred that the females do not scent the baits from such great distances as the males and are not sufficiently active to fly far.

There is very little accurate knowledge concerning the effects of different atmospheric and other environmental conditions on the readiness with which the moths are attracted to baits. It is usually considered that they come in greater numbers on dark nights than on moonlit ones and that still, thundery conditions are the most favourable. No good explanation for these tendencies has, however, been advanced. Seitz (1894) and Skertchly (1889) both observed that they were unable to attract moths to sugar in the tropics and this has been confirmed by other workers. Hering (1926 : 128) attributed this to the rich tropical flora, and pointed out that sugaring in temperate countries is most effective in early spring, late summer and autumn when fewest flowers are available.

9. Water.

(a) *The geographical distribution and environment of water-drinkers.*

The habit of water-drinking is very widespread among the Lepidoptera, and has aroused considerable interest owing to various peculiarities in the behaviour of the drinkers which remain at present without satisfactory explanation. A short review of the subject mentioning a few of the most outstanding records was included by Buxton in his review of insects and humidity (1932). Tutt (1897) gave a summary of the then existing knowledge of the subject, based both on personal observations and on those of other workers; to the latter, however, no bibliographical references are given.

Water-drinking has been recorded of a large number of species of Rhopalocera, and although the habit seems to be more prevalent in some families than

in others, all families are well represented if the records from different parts of the world be taken into consideration. Owing to the crepuscular or nocturnal habits of most of the Heterocera, very little is known of their habits with regard to water-drinking. Hering (1926 : 128) observed that in Germany the most numerous water-drinkers are Lycaenids but that even night-moths have been observed to drink; the only examples cited are the Sphingid *Hyloicus pinastri* L. and some unspecified SYNTOMIIDAE. The most extensive and indeed almost the only detailed observations on nocturnal drinkers are those of Collenette (1934), who collected the moths visiting damp sand in Matto Grosso, Brazil. 63 specimens of Noctuids, 8 Notodontids, 234 Geometrids, 5 Uraniids and 26 Pyralids were obtained. Seitz (1894) saw the Brazilian Sphingid *Macroglossa tantalus* L. flying from leaf to leaf and drinking dew-drops, ignoring meanwhile the flowers which were growing in the neighbourhood. Rothschild and Jordan (1910) recorded the capture by W. Hoffmans of large numbers of nocturnal Sphingids which were hovering over pools in Brazil. About 2500 specimens were caught over a period of several weeks; most of them belonged to the SESIINAE and nearly half to the two species *Pachylia ficus* L. and *P. resumens* Wlk. It does not appear that drinking was actually observed in these Sphingids, but it was taken for granted and it was stated that the moths drank so much water that jets of it spurted out when they were dissected. This habit of hovering over pools seems to be very prevalent in the SPHINGIDAE, and Mr. C. L. Collenette informs me that he observed it very frequently in Matto Grosso. I made some observations (Norris, 1934 B) on the Rhopalocera and diurnal Heterocera seen drinking on damp paths in the Alps. The Pyralids *Pyrausta funebris* Ström., *P. cingulata* L. and *Titanio phrygialis* Hb. were very abundant, and the Geometrids *Cidaria tristata* L. and *Ematurga atomaria* L. were also fairly frequently seen. Fassnidge (1924) saw the Geometrid *Halia brunneata* Thunb. drinking at wet mud in the Alps and also numbers of unspecified crepuscular Geometrids drinking in irrigation ditches; these were most abundant after particularly hot days. The experiments of Noyes (1930) claimed to show that the Phycitid moth *Ephestia elutella* Hb. is attracted to pure water in fairly large numbers, although more are attracted to fermenting sugar-baits. Johnson (1895) described a similar attraction of the flour-moth, *Ephestia kühniella* Z. to wet flour paste in mills. Trapping experiments with pure water, are, however, seldom carried out since fermenting baits are always more attractive. A certain amount of indirect evidence regarding water-drinking may be obtained from the findings of experimental workers who have shown that some Heterocera require water but not sugars for normal longevity and oviposition. The existence of such a condition has been shown in the Gelechiid *Sitotroga cerealella* Ol. (Simmons and Ellington, 1933), in the Phycitids *Ephestia kühniella* Z., *E. elutella* Hb. and *E. cautella* Wlk. (Norris, 1934 A), in the Crambid *Crambus teterrellus* Zinck. (Ainslie, 1917) and in the Tortricids *Cydia molesta* Busch. (Swingle, 1928), *Polychrosis botrana* Schiff. and *Clysia ambiguella* Hb. (Marchal, 1912). It may be supposed that these moths drink water under natural conditions if it is available. Thus Marchal (1912) found that the vine-moths when kept in captivity drink water with great eagerness and that, unless they do so, they die prematurely before ovipositing. It was further observed that the moths haunt the damper parts of vineyards and that they do not visit the flowers in the neighbourhood; the inference in this case is obvious. Ditman and Cory (1933) showed that the feeding-responses invoked in the Noctuid *Heliothis obsoleta* Fabr. on stimulation of the tarsal sense-organs by water, are exactly similar to those described by Minnich

in the butterflies *Pyrameis atalanta* L. (1922 A and B) and *Pieris rapae* L. (1924).

Fragmentary as is the evidence brought forward in the preceding paragraph, it does nevertheless suggest strongly that water-drinking is no less general among the Heterocera than among the Rhopalocera, and that the paucity of records concerning the former is due more to lack of observation than to their non-indulgence in the habit. The remainder of this section will be confined almost entirely to discussion of the phenomenon as it occurs in the Rhopalocera.

In Great Britain itself water-drinking is not practised with any regularity, but it has occasionally been observed on very hot summer days, chiefly in places near the South Coast. Adkin (1898) saw numbers of white butterflies following a water-cart on the parade at Eastbourne and settling to drink on the ground at intervals. Tutt (1897) recorded seeing *Pieris rapae* L. and *P. brassicae* L. drinking behind water-carts both in Deal and in the busy streets of Greenwich. He also saw a group of males of the Lycaenid *Polyommatus corydon* Poda drinking at a puddle near the South Foreland lighthouse. Longstaff (1905) saw a group of 14 or 15 *Pieris napi* L. drinking at wet mud at Morthoe in Devon. No records of drinking in more northerly parts of the British Isles have been traced.

Many writers have commented on the prevalence of the drinking-habit in Lepidoptera of the Alps. The swarms of butterflies which are to be seen drinking at damp spots on the mountain paths on any sunny summer day cannot fail to attract the attention of every entomologist. Comparatively few really detailed observations on the subject have, however, been published. The commonest Alpine drinkers are the Lycaenids, Pierines, and Hesperiids, but the habit is by no means confined to these families. Tutt (1897) commented in general terms on the swarms of blue butterflies which rise from the runnels crossing Alpine tracks, and also gave a few specific records. In the neighbourhood of Digne males of *Nomiades cyllarus* Rott. are commonly seen sitting on damp stones imbibing the moisture. On a path in Dauphiné the following butterflies were seen at a wet spot only one square yard in size:—3 *Papilio podalirius* L., 1 *Vanessa antiopa* L., 2 *Leucophasia sinapis* L., hundreds of *Polyommatus damon* Schiff. and *P. corydon* Poda, a few *P.* [*Lysandra*] *bellargus* Rott. and a few *P. astrarche* Bergstr. On another occasion enormous numbers of *P. corydon* Poda and *P. astrarche* Bergstr. were seen drinking in Dauphiné. Large numbers of the Geometrids *Cidaria populata* L. and *Larentia caesiata* Lang, were once found drowned in puddles after a stormy night in the Cogne valley; it was believed that they came to drink, and were unable to rise again during the storm.

My own observations on the Lepidoptera taken drinking on paths in the Austrian Tyrol have already been referred to in connection with the Heterocera. By far the most abundant of the Rhopalocera was the small Lycaenid *Cupido minimus* Fuess.; wherever drinkers were present this species was to be seen in enormous numbers. The larger Lycaenids seen drinking frequently belonged to the genera *Maculinea* and *Cyaniris*, *C. semiargus* Rott. being the commonest of these. Several other species were also observed. Very frequently seen among the drinkers were the Hesperiids of the genera *Pyrgus* and *Erynnis*. The only Nymphalid drinker was the Satyrine *Erebia euryale* Esp. Fassnidge (1924) observed numbers of unspecified Erebias on wet boulders beside an Alpine cascade. Most of my observations were made at altitudes of over 5000 feet, from which regions Pierines were absent, but *Pieris napi* L., *Leptidea*

sinapis L., and *Aporia crataegi* L. were seen drinking at places lower down the same valleys. At altitudes of over 6000 feet few butterflies were seen and assemblages of drinkers were consequently absent. Longstaff (1905 : 117) recorded seeing swarms of Lycaenids drinking at small puddles in the road in Germany; the species mentioned are *Lycaena alsus* Schiff., *L.* [*Maculinea*] *arion* L. and *L. baetica* L. *Apatura iris* L. was also caught drinking at the same place; Tutt (1897), Kane (1885 : 55) and Kirby (1882 : 24) all state that this butterfly is in the habit of settling on the ground to suck moisture. Goodman (1926) saw masses of Hesperiids sucking at wet mud on a river bank in the Cevennes. The commonest species was *Hesperia alveus* Hb., but *Carcharodus lavatherae* Esp., *Spilothris altheae* Hb., *S. alceae* Esp. and *Nisoniades tages* L. were also present.

The most important work on the water-drinking butterflies of the United States is that of Clark (1932) who studied in some detail the assemblages at roadside puddles in the district of Columbia. The commonest drinkers in this region are apparently the yellow Pierines *Colias philodice* Godt. and *Eurema lisa* Boisd. and Lec.; groups of this latter species consisting of from four to twenty individuals are seen. Scudder (1889 : 493) also remarked on the yellow butterflies which are seen ranged in hundreds along the edges of roadside puddles in New England. Species mentioned by Clark as being water-drinkers are the following :—

Pieridae. **Eurema lisa* Boisd. and Lec., **E. nicippe* Cr., **Phoebis eubule* L., **Colias philodice* Godt.

Papilionidae. **Papilio glaucus* L., **P. marcellus* Cr., *P. troilus* L., *P. polyxenes* Fab.

Lycaenidae. **Phyciodes tharos* Drury, **Everes comyntas* Godt., *Feniseca tarquinius* Fab., *Lycaenopsis argiolus* L.

Nymphalidae. *Basilarchia arthemis* Drury, *Junonia lavinia* Cr., *Polygonia comma* Harr., *P. interrogationis* Fab., *Vanessa antiopa* L., *Pyrameis virginiensis* Drury, *P. atalanta* L.

Hesperiidae. **Epargyreus tityrus* Fab., *Pholisora catullus* Fab., *Thorybes daunus* Cr., *Pyrgus tessellatus* Scud.

All the families of the Rhopalocera are thus well represented among the water-drinkers of this region. It should be noticed that none of the most characteristic drinkers belong to the family Nymphalidae. Several other points of interest concerning the habits of drinkers are brought out in this paper, but these will be discussed in the relevant sections.

The only other temperate region from which detailed records are forthcoming is South Africa, where some specimens drinking at mud were taken by Dixey and Longstaff (1907). Among those recorded were :—

Pieridae. *Belenois gidica* Godt., *B. mesentina* Cram., *Terias brigitta* Cram.
Nymphalidae. *Acraea alboradiata* Auriv., *A. atolmis* Westw.
Lycaenidae. *Axiocerces amanga* Westw., *Limnas chrysippus* L.

By far the greatest number of observations on water-drinkers has been made in tropical regions where great assemblages of conspicuous butterflies, most notably Pierines, are a common sight on the banks of streams, damp places on roads, etc. One of the classical descriptions of such an assemblage is given by Bates in 1863, *Naturalist on the River Amazon*, **2** : 227–228. He wrote :—"It was impossible to walk far without disturbing flocks of them

* The most characteristic water-drinkers.

[butterflies] from the damp sand at the edge of the water, where they congregated to imbibe the moisture. They were of almost all colours, sizes, and shapes; I noticed here altogether eighty species belonging to twenty-two different genera. It is a singular fact that, with very few exceptions, all the individuals of these varied species thus sporting in sunny places were of the male sex; their partners, which are much more soberly dressed and immensely less numerous than the males, being confined to the shades of the woods." Bates goes on to say that the yellow and orange Pierines belonging to seven species of the genus *Callidryas* were the most abundant. The same preponderance of *Callidryas* was remarked by Gibbs (1912) in the assemblages in British Honduras and Guatemala and by Rosenberg (1909) in Colombia. Next to these in order of abundance (in Bates's assemblages) were about twelve species of *Cybdelis*. *Callithea markii* Hew. was occasionally present. On some very calm days the small green Erycinids *Symmachia trochilus* Er. were seen literally swarming on the sand. Collenette (see Collenette, C. L., and Talbot, G., 1928: 400–9) made some extensive observations on the assemblages of drinkers in Matto Grosso, Brazil. As many as 2000 individuals were frequently seen in an assemblage, the commonest species being *Catopsilia statira* Cram. Four other species of *Catopsilia* were common as well as five other Pierines and twelve Papilios. Also mentioned were a *Libythea*, seven Nymphalids, two Lycaenids, an Erycinid and some unspecified Hesperiids. A number of observations made by Carpenter on the water-drinkers of tropical east Africa have been recorded at various times in the *Proceedings of the Entomological Society of London* (see Poulton, 1914, 1915, 1917 A and 1918). The information to be derived from these sources may be briefly summarised as follows :—As in Brazil, enormous assemblages, consisting principally of Pierines, often are seen drinking at wet mud. The predominant butterflies in these assemblages are species of *Pinacopteryx*, but species of *Belenois* and *Terias* are also exceedingly abundant. Other Pierines mentioned are *Teracolus*, *Mylothris*, and *Catopsilia*. Six species of *Papilio* were observed drinking as well as many Lycaenids and Hesperiids. The only Nymphalid recorded is *Atella phalantha* Drury. Dixey (1906) described a catch of 153 butterflies all taken with one sweep of the net while they were drinking at a pool near the Ripon Falls; 104 of the butterflies were *Pinacopteryx vidua* Butl. and the remainder belonged to two other species of *Pinacopteryx* and five species of *Belenois*. It seems that, speaking generally, these two genera of Pierines contribute the greatest proportion of drinkers to the assemblages of East Africa, just as *Callidryas* does to those in many parts of tropical America. Species of *Libythea* are also commonly seen drinking in large numbers (Poulton, 1927 A and 1921). It is well known that many Papilios drink water, and although they are perhaps not usually seen in such enormous numbers as the Pierines, they feature in most of the descriptions of African assemblages. Comparatively few of the records are specific, but enough evidence exists to show that the habit is indulged by a great variety of species belonging to this genus.

Longstaff (1905) recorded water-drinking in a number of species from India and Ceylon. The principal butterfly mentioned as drinking in dense groups is the Pierine *Catophaga paulina* Cram.; on one occasion a net put down over an assemblage at wet sand caught 38 individuals of this species, as well as 4 *Huphina* and 1 *Hebomoia*. Another abundant Pierine was *Catopsilia pomona* Fab. Six species of *Papilio* and a number of Lycaenids and Nymphalids are also mentioned. De Nicéville (1895) referred to the habit of water-drinking in connection with many of the species described. Analysis of

his records show that the occurrence of the phenomenon differs in no essential respect from its occurrence in south America, Africa, and India. Pierines are as usual predominant in the assemblages, the principal species being *Catophaga leis* Hb., *Catopsilia crocale* Cram., and nearly all species of *Terias*. The predominant Lycaenids are of the genus *Nacaduba*, of which all species are said to be particularly fond of water. Seven other species of Lycaenids and four Hesperiids are recorded. Special mention is made of the Nymphalids *Junonia atlites* Johanns., *Cyrestis irmae* Forb. and *Charaxes delphis* Doubl. and ten other species are recorded; this is an unusually large number for the family. Of Papilionids nine species of *Papilio* as well as *Leptocircus meges* Zink. and *Troides brookiana* Wall. are said to drink. This last species has been seen drinking in large assemblages in the Malay States (Poulton, 1925 A) and Kirby (1894) gave a translation from the Dutch of a paper by Piepers in which are described two remarkable flower-like assemblages seen in Celebes. One of the "flowers" was composed of two concentric rings of *Callidryas scylla* L. surrounding a group of white Pierines; the other was composed of *Pieris zarinda* Boisd., and other Pierines. Poulton (1911) recorded that in Borneo *Terias hecabe* L. often settles to drink in closely packed assemblages.

The foregoing summary of water-drinking as it occurs in different parts of the world is necessarily very fragmentary; there exist huge regions from which no records whatsoever are forthcoming. At the same time the evidence is sufficient for certain generalisations to be made with some degree of safety. In all regions where drinking occurs the predominant (diurnal) drinkers are nearly always Pierines. Where this is not the case, as at high altitudes in the Alps (see p. 72), it is probably due simply to absence of Pierines from the region as a whole. This usually unknown factor of abundance of individuals of a species in the region as a whole, has always to be taken into account before any estimation of the relative frequency of drinking between two species can be made. Judging from what is seen in the Alps, it would seem that the drinking-habit is at least as highly developed in the Lycaenids as in the Pierines; that it has been less commented on by observers in the tropics may be due to the Lycaenids being rendered less noticeable by the ubiquitous and more conspicuous Pierines and Papilionids. The habit is also undoubtedly very highly developed in this last mentioned family. In the NYMPHALIDAE, on the other hand, the habit is definitely less prevalent. In none of the descriptions of water-drinking do the members of this family feature to any great extent. It is true that De Nicéville (1895) and Clark (1932) describe a fair number of species as visiting water, but assemblages containing any number of individuals do not often seem to occur; most observers either record one or two odd captures or do not mention them at all.

The exact nature of the environmental factors which determine whether or not drinking shall occur in any particular region, are very little understood. The same species may be a habitual drinker in one region and not in another, so it is clear that the presence or absence of drinkers depends more on the environment than on the character of the local Lepidopterous fauna. That atmospheric conditions are important is demonstrated by the fact that, in any one region, drinking may occur on some days and not on others. Drinking is, speaking generally, more prevalent in the tropics than in temperate countries, and, in countries such as Great Britain, where it seldom occurs, the exceptions are always noticed on unusually hot days. Consideration of these facts points to the natural conclusion that drinking is induced by high temperature. But this explanation is insufficient to account for some peculiarities in the

distribution of drinkers. Simes (1934) pointed out that, although drinkers are common in the maritime Alps, they are not to be seen on the Mediterranean Coast of France. Nor have I ever observed butterflies drinking at the small Mediterranean springs which are so much frequented in summer by the Hymenoptera of this excessively arid region. Sheldon (1934) comments on the rarity with which butterflies are seen drinking in Trinidad. It is the existence of such anomalies which make it impossible to discern any simple relation between temperature and the occurrence of drinking. Nor is the position much simplified if the question of atmospheric humidity be considered. Speaking generally the Alps definitely provide a much damper environment than the Mediterranean coast during the summer months. A glance at the vegetation of the two regions is sufficient to show that this is true. Nevertheless it seemed possible that, on a hot and sunny day, the relative humidity of the atmosphere may be lower at high altitudes than at low ones near the sea. But examination of the very insufficient meteorological data which are available gave no striking confirmation of this idea. It is likely that the phenomenon might be better related to saturation deficiency than to relative humidity; but the necessary data for testing this point are not available. In any case drinkers are seen in the Alps when the sun comes out soon after heavy rain when, according to any standards of measurement, the atmosphere must be infinitely damper than it could normally be during a summer month in the Mediterranean. Moreover, Collenette (1928) mentions that Brazilian assemblages were more abundant after heavy rain. These considerations serve to show how badly in need of investigation are the problems concerned with the occurrence of water-drinking.

(b) *The behaviour of the water-drinkers.*

The tendency for the water-drinking Lepidoptera to congregate in closely packed assemblages at drinking places has always attracted much attention. This tendency is well marked in Pierines, Lycaenids, Papilionids and Hesperiids, all of which sometimes form groups of their own and sometimes come together in mixed assemblages. Similarly groups may be formed all of one species or, as is more frequent, of several species. I have described in detail (1934 B) the composition of some of the assemblages in the Austrian Tirol. The bulk of the assemblages at high altitudes in this region is formed by Lycaenids, but at lower altitudes Pierines are present. The diurnal Heterocera seen drinking were almost all solitary, the only exception being the Geometrid *Cidaria tristata* L. which was often seen in the assemblages. The typical assemblage-makers are of course sometimes seen drinking in solitude, but this is probably less usual in Pierines than in members of other families. Clark (1932) drew a definite distinction between the typical " puddle-butterflies " which assemble together at puddles and what he termed the " roadside-butterflies " which are fairly often seen drinking, but never in groups. Collenette (1928) divided the butterflies caught at damp sand in Brazil into several categories according to their behaviour with regard to assemblage formation. The categories being as follows :—(1) Those which make up the main bulk of the assemblages and settle together without distinction of species—these were all Pierines. (2) Those which either mix indiscriminately with the main assemblage or form gatherings of their own—five species of *Papilio* and one of *Terias*. (3) Those which form gatherings of their own on the outskirts of the main assemblage or apart from it—the Nymphalid *Megalura*, an Ericynid, two Lycaenids and

some Hesperiids. (4) Those which either form groups of their own or drink in solitude—four species of *Papilio*, one of *Libythea*, and one of the Nymphalid *Haematera*. (5) Those which usually drink in solitude—these were all Nymphalids and Hesperiids. Experiments with dead decoy specimens of the Pierine *Catopsilia* indicated that the formation of the assemblages depended largely on a visually-determined instinct to crowd together; it was inferred that other factors must be at work in determining the choice of drinking spot in the case of less constant assemblage-formers. Clark (1932) also found that when a dead, yellow Pierine, or even a piece of yellow paper, was thrown down on the mud, a group of butterflies soon assembled round it. These observations are quite compatible with what is known concerning the importance of sight in the finding of flowers by Pierines (see p. 65). It is probable that flower-visiting and assemblage-formation are two manifestations of the same instinct. How far the choice of a drinking-spot by the *originator* of the assemblage depends on chance and how far on definitely attractive properties of the water at the spots in question, is a matter of some doubt. Butterflies are frequently seen to return persistently to the same patch of ground after having been disturbed, and it may be supposed that in these instances some definite chemical attraction must be at work. This point, however, may better be discussed in a later section.

Butterflies, at least in the Alps, drink only when the sun is shining; the assemblages disappear at once when the sun goes behind a cloud. They are most numerous on the hottest day (Norris, 1934 B). Collenette (1928) observed that the Brazilian drinkers were most numerous on hot sunny days after rain, and that although they begin to appear at about 11.0 a.m. they only reach their maximum at 1 p.m. There are several records of butterflies drinking without intermittance for very long periods. Dukinfield Jones (1883) saw the Brazilian Geometrid *Panthera apardalaria* Wlk. drinking on wet stones in the bed of a flowing stream. The moths were drinking continuously and at the same time exuding droplets of water from the anus at the rate of fifty per minute. The same moth was observed to drink for three hours, and it was calculated that about 200 times the volume of the body in water must have passed through the alimentary canal during this time. Baron (1884) observed numbers of *Papilio oribazus* Boisd. and of the Pierine *Appias saba* Fab. behaving in the same manner on the bank of a stream in Madagascar. Layard (1883) also observed it in several species of *Callidryas* and *Pieris* in Ceylon and in *Papilio demoleus* L. in South Africa. Skertchly (1889) saw the Papilionid, *Leptocircus curius* Fab., pumping water out of the anus in rhythmical squirts reaching as much as three inches. How far such prolonged drinking accompanied by exudation of water from the anus is the rule is doubtful, since few observers record having watched individuals for any length of time.* Nor is the physiological significance of this behaviour understood. It has been suggested that the passage of water through the body has a necessary cooling effect, or that nutriment is extracted from the water during its passage through the alimentary canal. Dukinfield Jones, however, pointed out that the water of the Brazilian stream where his observations on *Panthera* were made, was extremely pure and clear.

Lepidoptera have on several occasions been seen to settle actually on the surface of water—not merely on damp places. Joannis (1901) saw a crowd

* Mr. C. L. Collenette informed me that he never observed water being exuded from the anus in the Brazilian assemblages; the sandbanks in this instance were not, however, very wet.

of unspecified Pierines resting on the surface of a river, flying off and returning again to settle at intervals; it was not clear, however, whether the butterflies were drinking or merely bathing. Poulton (1932) records that the Sphingid *Deilephila euphorbiae* L. was twice seen to alight on the surface of a pool at Quetta; the first time it hovered over the surface with rapidly vibrating wings, but the second time it actually rested on the water with outspread wings. Some Crambids and Pyralids have been observed to alight on the surface of the open sea, but this habit is regarded as being an aid to migration and it is unlikely that any question of drinking is involved (Poulton, 1909, 1928).

(*c*) *The sex of water-drinkers.*

One of the most interesting and the least understood features of the water-drinking problem is the greater development of the habit among males than among females. In a regrettably large proportion of the records the sex of the butterflies is not mentioned or the subject is dismissed with a vague remark to the effect " that, as is well known, the drinkers are always males." Such comments are unreliable to a degree, since the presence of a minority of females would probably pass unnoticed by an observer whose ideas on the subject were preconceived. At the same time sufficient detailed evidence exists to show that the habit of drinking in open places is very much commoner in males than in females. Of the 153 Pierines caught in one sweep of the net near the Ripon falls (Dixey, 1906) not a single one was a female. Longstaff (1905) saw clusters of 20 or more *Catophaga paulina* Cram. drinking at damp sand; all of these were males. The butterflies described by Bates (1863) were, *with a few exceptions*, all males. De Nicéville's records of water-drinking concern the males only, and he says of nearly all the species that the males assemble to drink at moist spots but that the females keep to the forest. This restriction of the females to the forest has been noticed by all tropical Lepidopterists. An outstanding exception to the general rule was reported by Carpenter (see Dixey, 1915) who remarked that both males and females of the Pierine *Leuceronia thalassina* Boisd. assemble to drink at moist spots. This is the only definite record of female Pierines taking a significant part in assemblage formation that has been encountered. Collenette (1928) throughout his work on the Brazilian drinkers only took the following females at damp sand :—

Pieridae. 1 *Daptoneura lysimnia* Fabr., 1 *Catopsilia statira* Cram.
Papilionidae. 1 *Papilio thoas* L.
Lycaenidae. 2 *Leptotes cassius* Cram.
Nymphalidae. 1 *Haematera pyramus* Fabr.

Dixey and Longstaff (1907) took at wet mud single females of *Terias brigitta* Cram., *Acraea alboradiata* Auriv., and *A. atolmis* Westw. Longstaff (1905) took three females of the Nymphalid *Euthalia garuda* Moore at wet mud. All the butterflies caught by me (1934 B) in the Alps were males, but Simes (1934) saw several female Satyrines belonging to nine species drinking near Digne. Some females of the Pierine *Aporia crataegi* L. and of the Lycaenid *Plebeius argus* L. were also seen drinking. Simes observed that most of these females were old and worn and they were solitary, not in assemblages. These observations agree with those of Clark (1932), who remarked that the occasional females seen at the Columbian puddles were very worn and that the males paid no attention to them.

The same preponderance of males over females was seen in the Heterocera taken drinking at damp sand by Collenette (1934). Of 63 Noctuids taken, 6 specimens were females, and of 234 Geometrids, 2 specimens were female. Of 26 Pyralids, 1 was female. Of about 30 diurnal Heterocera taken in the Alps only one Pyralid was a female (Norris 1934 B). The Sphingids taken by Hoffmanns hovering over pools in Brazil (see Rothschild and Jordan 1910) were practically all males. Hampson (1900), on the other hand, saw an enormous assemblage of the Pyralid *Oligostigma arealis* Hmpsn. in Ceylon, and the sexes here were present in equal proportions.

Various theories have been advanced in explanation of this curious sexual difference in habit, but none is entirely satisfactory since they are all based on supposition only and not on experimental evidence. The most obvious, and at first sight the most reasonable theory, is that of Poulton (1906), namely that the males fly about more actively in the sun than do the females and consequently have more need of moisture. This may be so in the tropics where the females of the species concerned are found only in the forest and not in the open places with the males. But it is difficult to imagine that this factor can be very important in such an open habitat as the Alpine meadows, where the females must necessarily fly about actively in the sun both for purposes of feeding and of oviposition. Moreover, it is well known that in temperate countries both males and females of such butterflies as the Pierines spend much of their time on the wing flying from place to place. Personal observations on *Pieris rapae* L. showed that the females fly rapidly from one place to another, pausing to flutter over each patch of plants, laying an egg if a suitable crucifer happens to be present, and then passing on to the next. It is improbable that the lives of the males can be very much more active than this. If the females can obtain sufficient moisture from the nectar of flowers, there is at least no *a priori* reason why the males should not do likewise. My experiments (Norris, 1935 B) showed that male Pierines, no more than females, can live normally without sugars, even if water is supplied to them; so there can be no question of the water serving as an easily obtained substitute for nectar. Exact observations on the relative frequency with which flowers are visited by the two sexes would be of the greatest value in this connection. It is difficult to avoid considering the likelihood that the male butterflies may have developed a habit from which they obtain no benefit. It is surely unreasonable to deny that the development of such a habit is a biological possibility. An entomological precedent for such a state of affairs is afforded by the Mediterranean Fruit Fly, *Ceratitis capitata* Wied., the males of which are attracted in large numbers to ordinary kerosene, while the females are not attracted at all (Severin and Severin, 1913). Moreover, even if water were beneficial to both sexes, it could readily be understood that the females might be prevented, in the interests of survival, from developing a habit which would involve their being diverted from the breeding-grounds. It must be remembered that although the females do not join the assemblages, there is no evidence to show that they do not drink water in solitude amongst the herbage. Clark (1932) considers that the puddle-butterflies represent the newly emerged immature males from overpopulated areas, which, driven away by the older males, resort to the puddles where (in the absence of the females) they cease to be pugnacious and become gregarious. This idea is based on his observation that the drinkers are nearly always fresh-looking, whereas the males which are found in the surrounding fields are worn and battered. Clark also states that drinkers are never seen unless the species is common in

the vicinity and that in a certain very dry year, when the numbers of all butterflies were reduced, none at all were seen at the puddles. This theory is interesting, but the evidence in favour of it is somewhat circumstantial, and many detailed observations on the behaviour of the butterflies and exact computations of the sex-ratios at different times would be necessary in order to render it fully convincing.

10. Animal Excreta (Dung, Perspiration, etc.).

Dung-visiting, like water-drinking, is not regularly practised by the Lepidoptera of Great Britain, but it does sometimes occur on exceptionally hot days. Little has been published concerning British butterflies visiting dung, but personal information seems to show that those most frequently seen on dung are the Lycaenids *Lysandra bellargus* Rott. (the Adonis butterfly) and *Polyommatus corydon* Poda and the Nymphalid *Apatura iris* L. This last species has a particularly noticeable attraction to dung as it has also to carrion, rotten cheese and other strongly smelling, putrid substances. I recorded (Norris, 1935 A) seeing several specimens of *Pieris rapae* L. and *P. napi* L. as well as some Lycaenids on dung.

Although the majority of butterflies seen drinking in the Alps are settled on the bare soil of paths, they often settle and feed actually on the patches of dung. This applies alike to Pierines, Lycaenids, Papilios and Hesperiids. Seitz (1894) mentions *Apatura*, *Vanessa* and *Limenitis* as being characteristic dung-visitors. The Satyrine Erebias are particularly attracted to dung (Tutt, 1897; Norris, 1934 B) and my observations showed that they normally formed groups of their own on patches of dung. It was only on one particularly hot day that they were seen drinking on the bare soil in company with members of the other families. It was further remarkable that, whereas the dung visited by the Erebias was often old and dried, that visited by the other butterflies was usually fresh and moist. Hering (1926 : 129) says that when the dung is dry the butterflies moisten it with a drop of fluid from the anus and then suck this up again. I, however, watched the Erebias while they were feeding on the dung and was never able to detect the use of this device. It is probable that Hering had in mind the Hesperiids which are well known to behave in this way when attracted to human perspiration on skin, clothing, and furniture. The principal species of which this habit has been recorded are the African Hesperiid *Rhopalocampta forestan* Cram. (Farquharson, 1921; Poulton, 1925 B) and the Alpine *Augiades sylvanus* Esp. (Richards, 1930; Dietze, 1921). The latter species was once observed to perform the same actions when attracted to a drop of dried ink (Poulton, 1913), and Kühn (1887) observed it in two Hesperiids settled on a piece of dried bird-dung. The Alpine Erebias are also very commonly attracted to sweat (Seitz, 1894; Dietze, 1921; Norris, 1934 B), but the habit has been more discussed in relation to the Hesperiids on account of their curious mode of feeding. Collenette (1928) captured a number of Nymphalids and Hesperiids at sweat on clothing in Brazil; only the Hesperiids exuded the droplet of water, none of the Nymphalids were observed to do so, although the sweat was perfectly dry. There seems to be little doubt that this habit, so characteristic of the Hesperiidae, is not shared by the Nymphalidae. It is reputed to have been observed in a Lycaenid of unknown species (Poulton, 1917 B), but it was suggested that the butterflies in question may really have been Hesperiids. Kirby (1882 : 24) records the attraction to sweat of large numbers of *Apatura iris* L. in Germany.

Standfuss (1884) describes a remarkable swarm of Psychids attracted to sweat in Italy, about thirty individuals belonging to two species of *Psyche* being present; he saw similar gatherings on several other occasions. Oberthür (1876) wrote that the Pierine *Anthocharis charlonia* Donz. is attracted to sweat of horses in Algeria. There exists a large number of rather vague records concerning the attraction of tropical butterflies to dung and sweat, but only a few of the more definite ones can be mentioned here. Carpenter (see Poulton, 1918) took the following Pierines on a patch of cow-dung in east Africa :— 8 *Belenois mesentina* Cram., 5 *B. severina* Cram., 2 *Pinacopteryx simana* Hopff., 1 *Teracolus eris* Klug, 1 *Herpaenia eriphia* Godt. and 1 *Glutophrissa epaphia* Cram. Poulton (1927 B) records the attraction to water contaminated with leopard-dung of the following east African butterflies :—*Papilio nireus* Cram., *P. bromius* Doubl., *P. dardanus* Brown, *Aspenetheus lormieri* Dist. and *Charaxes* spp. On the same occasion large numbers of the Nymphalid, *Crenis* sp., were attracted to human sweat. Longstaff (1905) observed an enormous assemblage of butterflies at a wet halting-place of bullocks in Ceylon; one sweep of the net took 50 *Catophaga paulina* Cram. as well as some odd Nymphalids. Pryer (1884) describes how the guano impregnated water running out from a cave in Borneo was frequented by many butterflies of the genera *Papilio* and *Pieris*. Comparison of these observations with those on the *water-drinkers* in the corresponding parts of the world demonstrates the essential similarity between the two sets of records. Sumatran butterflies which have been known to settle in large numbers on sweat are the Nymphalids *Euploea ochsenheimeri* Luc. and *Cynthia juliana* Cram. (Forbes, 1885). De Nicéville's Sumatran record provide an interesting parallel with those from the Alps. It is found that, whereas many members of nearly all families are said to frequent wet spots on roads, it is particularly the Nymphalids which are described as definitely coming to faeces on the roads. There is little doubt that, while members of all families are attracted to water and damp soil contaminated with animal excreta, the Nymphalids are more surely guided to the actual faeces or main source of the contamination. It is probable that this is due to their having a more finely developed olfactory sense; that they find their *sugary* foods by scent to a greater extent than other butterflies has been demonstrated by Knoll and Ilse (see p. 65). Reasons for considering that their visual instinct for assemblage formation is, on the other hand, less developed than that of other butterflies have already been discussed (see p. 65), and it may be supposed that on this account their attention is less diverted from the actual source of the scent than is the case with members of other families.

The observations of Collenette (1928) on the butterflies visiting damp sand in Brazil (see p. 82) are of the greatest importance in connection with the problem of the visits of Lepidoptera to animal excreta. It was noticed that the assemblages on the river banks were always formed at fords or at places where clothes were washed; huge stretches of mud intervening between these places were not frequented by the butterflies, although apparently equally suitable for drinking purposes. The washing-places seemed to be particularly frequented, and a similar attraction has been occasionally recorded by other workers; thus Swynnerton (see Poulton, 1921) records seeing numbers of African Libytheas settling at a washing-place and suggested the possibility that the alkali of the soap was sought after. Collenette carried out some very interesting experiments which showed that the soap itself was not attractive, but that if a handkerchief soaked in perspiration was dipped in water and

then squeezed out on a sandbank frequented by butterflies, that particular spot on the sandbank soon became the greatest centre of attraction. It was found, on the other hand, that if a similar spot was prepared on an *unfrequented* sandbank, it was not usually discovered by the butterflies unless a dead decoy butterfly was thrown down as well. In some experiments such decoys were put down alike on treated and untreated patches of sand; the butterflies were attracted in both instances but they only remained to form the nucleus of an assemblage in those places where perspiration was present—in the other places they simply tested the soil with the proboscis and then flew off again. It was therefore obvious that, at least in the case of the principal assemblage formers, the originator of the assemblage finds a suitable place by means of trial and error, and that the newcomers are visually attracted by the presence of other butterflies. That is to say the olfactory sense is apparently not employed at all in the choice of drinking-places. Passing butterflies were only attracted to an assemblage if they came within seven yards of it; Mr. Collenette informs me that this distance was accurately measured and suggests that its constancy affords further proof of the importance of sight. In spite of this it was observed that at the beginning of each day the originators of the assemblages *did* tend to alight and test the soil at the fords and washing-places; this was considered to be due to some memory of the previous day's assemblage, but it seems equally possible that it may be attributed to the operation of some rather inaccurate olfactory sense acting as a vague attractant to neighbourhoods where the contamination is particularly concentrated. That scent is not of prime importance was, however, further shown by the fact that garments soaked in perspiration and hung up on frequented sandbanks did not themselves attract any of the assemblage-forming butterflies; only the treated sand was attractive. It was nevertheless possible to attract certain Nymphalids and Hesperiids to such garments when hung up in the forest, and in these instances it was thought that scent must be involved. The latter captures were comparable to those of Nymphalids and Hesperiids so often recorded from other parts of the world, and there is no doubt whatever that an olfactory sense is employed by these butterflies when they are attracted to sweat on animals and human clothing. That a great proportion of such visits should be made by Nymphalids only bears out what has already been said concerning the olfactory sense of the members of this family.

Collenette was also able to attract large numbers of Brazilian nocturnal Heterocera to perspiration-soaked objects as well as to damp sand; the details of these experiments were published in a later paper (Collenette, 1934). The attraction of Heterocera to damp sand has already been discussed (see p. 76), but it should be mentioned here that they showed the same preference for fords and washing-places as the butterflies, but they were scattered about in the favoured spots rather than packed in crowded assemblages. The following specimens were taken on perspiration-soaked objects :—

Family.	No. of males.	No. of females.
Arctiidae.	21	—
Agaristidae.	3	—
Noctuidae.	704	314
Notodontidae.	95	2
Geometridae.	418	13
Uraniidae.	17	—
Thyrididae.	8	—
Pyralidae.	84	—

The preponderance of Noctuids is comparable with their preponderance at fermenting sugars, and may be attributed to their particularly well-developed olfactory sense. The high proportion of female Noctuids is remarkable since, with the exception of the six specimens already mentioned (see p. 78), all the Brazilian Rhopalocera taken at perspiration were, as is usual with water-drinkers, of the male sex. It was further noticed that, on any one night, practically all the specimens of a particular species were of the same sex; that is to say all males of a species would come on one night and all females on others. For various reasons this curious fact could not be referred to sexual differences in dates of emergence or hours of flight, and no satisfactory explanation of it was forthcoming. It is doubtless owing to their nocturnal habits that there are so few other records of Heterocera visiting sweat or dung. Fassnidge (1924) observed numbers of the diurnal Geometrid *Halia brunneata* Thunb. attracted to human sweat, and Norris (1934 B) took one male each of the diurnal Pyralid *Titanio phrygialis* Hb. and the Torticid *Argyroploce mygindana* Schiff. at sweat. Dewitz (1911) observed that the Tortricid *Clysia ambiguella* Hb. is attracted to those parts of vineyards where dung is present.

The assemblages of butterflies described by Collenette are perfectly typical, both as regards species and sexes, of the water-drinking assemblages noticed by other tropical observers, and the likelihood that many, if not all, assemblages may be attributed to contamination of the water by dung or sweat is very great. It is, of course, hardly possible to draw any distinction between the two types of contamination, as traces of sweat are probably left behind wherever animals have been recently; Collenette found that a very small trace might act as an effective attractant. Here may be an explanation of the virtual restriction of the assemblages to the pathways in such regions as the Alps, where I never saw a single drinker except on or beside roads or paths. There could be no question of the paths being the only places where water was available, as in many localities, especially after rain, the surrounding hillsides were streaming with water. It remains to be proved that butterflies are *never* attracted to pure water, but the arguments against this taking place with any frequency are very considerable. It must be remembered that the vast majority of observations are made in places where animals or man are likely to have been, and, where this is not true, it is under no circumstances possible to be sure that the water is uncontaminated unless chemical analysis is undertaken. These considerations are, however, without prejudice to the problem concerning the physiological need which is satisfied by the drinking-habit. It has been suggested that the attraction of Lepidoptera to animal excreta is due to their need of certain salts, possibly of sodium chloride (Poulton, 1917 B). Skertchly (1889) described how numbers of Bornean *Papilio*, *Catopsilia*, *Terias* and *Charaxes* were attracted both to plain salt and to salt fish soaked in water and laid out on the sand to dry. Collenette (1928), on the contrary, observed that the salt put out for cattle in Brazil never attracted any butterflies, although it was often quite moist. There exists, at the other extreme, the possibility that the insects are really only in search of moisture but that, water being odourless, they are attracted to it only when contaminated with the highly-smelling substances which they have come to associate with its presence. Here we should have an exact analogy with the attraction of some Lepidoptera to fermenting sugars in adaptation to their need for the odourless and therefore unattractive sugar. This question of associative attraction has been previously discussed (Norris, 1934 A). There remains to

be considered the possibility that the development of the habit is accidental and non-adaptive. These problems can only be solved experimentally, and, pending the carrying out of such work, further speculation on the subject is without value.

Dung and perspiration are not the only animal excreta which have been known to attract Lepidoptera. The Noctuid moth *Arcyophora longivalis* Guén. has the singular habit of feeding on the moisture exuding from the eyes of cattle (Marshall, 1915; Brain, 1929 : 257), on account of which it is believed to be instrumental in transmitting ophthalmia. Shannon (1928) records the attraction of a large number of nocturnal moths to the secretions of horses' eyes in the Argentine. These included eight species of Geometrids, a Sphingid, a Notodontid and a *Pyrausta*. Some of the moths were seen to be feeding simply on the sweat, but it was suggested that they were really attracted by the light reflected from the animals' eyes. *Polygona c-album* L. has been seen sucking the blood of a wounded horse (Seitz, 1894), and a number of African moths were once found sucking the moisture from a wounded buck (Marshall, 1915). Human saliva is sometimes said to be attractive to butterflies. Tümler (1885) found that *Pieris brassicae* L. when kept in captivity would feed on saliva in preference to sugar solution. De Nicéville (1895) reported that Sumatran species of the Nymphalid *Mycalesis* are often attracted to the saliva of the betel-chewing natives.

11. Summary and Conclusions.

The principal source of food of the adult Rhopalocera is the nectar of flowers; this fact is too well known to require much discussion. How far the same is true of the adult Heterocera is exceedingly doubtful. It is certain that flowers are visited by a large proportion of the Noctuidae, a smaller proportion of the Geometridae, most of the Sphingidae, and by the Lithosiine group of the Arctiidae. Very little is known concerning the feeding-habits of the Microlepidoptera; there are only a very few definite records of flower-feeding, but no generalisations as to its relative frequency in different families can be made. It has been shown that many butterflies (particularly Pieridae and Papilionidae) find flowers entirely by the exercise of their powers of vision, whereas in others (particularly the Nymphalidae) the olfactory sense is more important. It has also been shown that even a nocturnal moth may find flowers by sight and not by scent.

There is a number of highly-smelling sugary substances besides flower-nectar which are frequently fed upon by those Lepidoptera which have a highly developed olfactory sense. These include the juices of rotting fruit, the exuding sap of wounded plants, the honeydew of aphids and the artificial sugar-baits used by entomologists. The principal visitors to such sources of food nearly always belong either to the Noctuidae or to the Nymphalidae, but they are occasionally joined by members of other families. Since these substances can only be detected by their smell they are only attractive when in a fermenting state. The habit of honeydew-feeding indulged in by certain Lycaenids is of rather a special nature, arising as it does probably from their association with honeydew-feeding ants during their larval life. A number of Noctuids are known to pierce the rind of sound and even unripe fruit in order to suck out the juices. In some of these species the proboscis is modified in adaptation to this mode of feeding, but it is doubtful whether or not this is

always the case. A few Nymphalids are known to behave in a similar manner. A curious aberration is seen in the Sphingid, *Acherontia atropos* L., which obtains its sugars by robbing the honey from bee-hives. So far as positive records go, it seems that all these sugary substances are visited to an equal extent by the two sexes.

It is well known that a large number of Lepidoptera have the habit of water-drinking very highly developed. The regular occurrence of this phenomenon is restricted to certain parts of the world; it is most noticeable in the tropics and is also exceedingly prevalent in the Alps, but it does not occur in the more northerly temperate countries except in unusually hot weather. The exact nature of the environmental and atmospheric conditions governing its occurrence are very little understood. For various reasons the habit has attracted most attention in the Pierines, but it seems to be equally developed in the Papilionids, Lycaenids, and Hesperiids; it is probably less developed in the Nymphalids. Certain Heterocera are known to drink, but very few records are available. The water-drinking butterflies tend to settle together in closely packed assemblages, either of the same or of different species. The bulk of most of the assemblages is formed of Pierines except in districts from which they are absent, when Lycaenids may predominate. The Papilionids and Hesperiids also form assemblages, but the tendency is less developed in the Nymphalids. Such water-drinking is almost entirely confined to the male sex, and the presence of females in these assemblages in open places must definitely be regarded as exceptional; the possibility that the females may drink water independently from the males and not in assemblages has to be considered. The problem of water-drinking in the Lepidoptera is inextricably confused with that of their attraction to the dung and perspiration of animals and human beings. There is some reason to believe that practically all water-drinking may be primarily due to such attraction. It has been definitely shown, at least in one instance, that the formation of a series of perfectly typical water-drinking assemblages, involving members of all the principal families, could be traced to the presence of human perspiration in the soil. It is also true, firstly, that most observations have been made in places where animals and man may have been present, secondly, that in such localities as the Alps it has definitely been observed that the drinkers are virtually restricted to pathways and roads, and, thirdly, that butterflies are very frequently observed to settle and feed on actual patches of dung.

Such evidence as exists seems to show that Lepidoptera may be attracted to animal contamination in two different ways. In the Pierines, for instance, the originator of the assemblage has been shown to find the suitably contaminated patch of soil by methods of trial and error; when the spot is selected this butterfly settles down to drink and the newcomers are attracted to it entirely by sight. In the Nymphalids, on the other hand, the visual assemblage-forming instinct is usually less developed and the power of smelling the substances at a distance is exercised. This is shown by the particular tendency of members of this family to visit perspiration on the human skin and clothing as well as the actual patches of dung lying in a generally contaminated area; they are more accurately guided to the actual source of the scent than other butterflies. The HESPERIIDAE seem to occupy an intermediate position in this respect between the NYMPHALIDAE and the principal assemblage-forming butterflies.

The problem of the physiological needs, if any, which are satisfied by the drinking of water, pure or contaminated, remains entirely uninvestigated.

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